Seasonal Distribution of Fall Armyworm (Lepidoptera: Noctuidae) Host Strains in Agricultural and Turf Grass Habitats

ROD N. NAGOSHI[1] AND ROBERT L. MEAGHER

Center for Medical, Agricultural and Veterinary Entomology, Agricultural Research Service, U.S. Department of Agriculture, Gainesville, FL 32608

Environ. Entomol. 33(4): 881–889 (2004)

ABSTRACT Male fall armyworm moths [*Spodoptera frugiperda* (J. E. Smith)] were captured in pheromone traps over a 16- to 24-mo period in selected sites in southern Florida. Molecular markers were used to determine whether individuals were of one of two host strains (historically designated "rice-strain" and "corn-strain"). Traps placed in agricultural areas showed a population peak in the spring (March–May) and fall (October–December), with a prolonged decline in numbers in summer (July–October) and a smaller reduction in mid-winter (January). The host strain distribution during these periods varied significantly, suggesting strain-specific and seasonal population patterns. Both strains were captured in substantial numbers during the spring peak, but surprisingly, only the rice-strain showed an increase in capture rates during the fall, despite the presence of sweet corn throughout this period. Trap captures in a sod (turfgrass) farm were composed almost entirely of the rice-strain and showed a bimodal seasonal distribution similar to that seen in the agricultural areas, with peaks in the spring and fall. These results represent the first indication that the two host strains might have substantially different population dynamics in the overwintering agricultural areas of Florida and suggest that the rice-strain is the predominant fall armyworm pest during the fall and winter growing periods. It further indicates that the two strains can display a markedly different response to seasonal environmental cues. The implications of these findings on our understanding of fall armyworm migration are discussed.

KEY WORDS fall armyworm, *Spodoptera frugiperda*, host strains, population dynamics

FALL ARMYWORM, OR *Spodoptera frugiperda* (J. E. Smith), is periodically a significant pest of maize, sorghum, forage grasses for livestock, turf grasses, rice, cotton, and peanuts, and whose range extends from southern Canada to much of South America (Luginbill 1928, Sparks 1979). Complicating our understanding of fall armyworm field behavior is the existence of two sympatric and morphologically identical strains (Pashley et al. 1985). The strains were identified by molecular polymorphisms and defined by their host plant preferences, hence their designation as "host strains" (Pashley 1986). The rice-strain (R-strain) is typically found on rice and Bermuda grass, whereas the corn-strain (C-strain) prefers field and sweet corn. The two strains can be distinguished by strain-specific allozyme variants and genetic markers (Pashley 1989, Lu et al. 1992, 1994, Lu and Adang 1996, McMichael and Prowell 1999). Host strains differ in larval development on host plants (Pashley 1988, Pashley et al. 1995), mating behaviors (Pashley and Martin 1987, Whitford et al. 1988, Pashley et al. 1992), use of food resources (Veenstra et al. 1995), resistance to certain pesticides (Pashley et al. 1987a), and susceptibility to different plant cultivars, including transgenic *Bacillus thuringiensis* Berliner plants (Pashley et al. 1987b, Jamjanya et al. 1990, Quisenberry and Whitford 1988, Adamczyk et al. 1997). Clearly strain-specific differences have important ramifications toward the development of effective control strategies, yet virtually nothing is known about the behavior of the two strains in the field.

Fall armyworms are not known to diapause and so cannot survive the winters in temperate climes. This means that the infestation of much of the United States originates entirely from populations overwintering in southern Florida, southern Texas, and northern Mexico (Luginbill 1928, Mitchell 1979, Sparks 1979, Pair et al. 1986, Raulston et al. 1986). Population surveys in southern Florida indicate a rise in the fall armyworm population in the spring, followed by a rapid and prolonged decline during the summer months (Pair et al. 1986, Mitchell et al. 1991). This decline corresponds to, and presumably reflects, the northward migration of this population into northern Florida and southern Georgia in April and May (Snow and Copeland 1969, Greene et al. 1971), which continues into the northern states by July and August (Mitchell 1979). It is speculated that this migration allows fall armyworm to

[1] E-mail: rnagoshi@gainesville.usda.ufl.edu.

0046-225X/04/0881–0889$04.00/0 © 2004 Entomological Society of America

avoid adverse weather conditions deleterious to host plant development and to escape density-dependent natural enemies (Knipling 1980). However, the environmental factors that trigger migratory behavior are unknown.

If habitat-specific factors initiate migration, we might expect the two host strains to differ in the timing of their northward movement. In particular, the behavior of the corn-strain should be influenced by the planting and harvesting cycle for corn, whereas the rice-stain would more likely reflect seasonal changes occurring in grasslands. Some evidence of strain-specific differences in population dynamics were observed in Louisiana, with the two strains showing peak pheromone capture rates at different times of the year (Pashley 1988, Pashley et al. 1992). This could indicate differences in the timing of the migration of the two strains into the tested area.

We are currently studying the distribution of fall armyworm strain populations in southern Florida using pheromone traps. Trap captures at three sites were examined in particular detail because their respective plant populations allowed clear predictions as to which strain should predominate. We found evidence for substantial and consistent differences in the seasonal population dynamics of the two strains even in collections made from the same location. The implications of these results on our understanding of fall armyworm migration and population behavior are discussed.

Materials and Methods

Trap Collection and Sites. We used pheromone traps in three southern Florida locations to estimate seasonal changes in population density during an 18-mo period from January 2002 to July 2003. Male adult moths were captured in pheromone traps placed adjacent to a sweet corn field, a mixed agricultural area with nearby tomato and sweet corn plantings, and a sod farm growing turfgrass. We anticipated that the corn-strain would predominate during the growing seasons for the first two locations, whereas the rice-strain would be the primary population in the sod farm. Adult males were collected using pheromone traps as previously described (Meagher and Gallo-Meagher 2003). Standard plastic Unitraps were baited with a commercially available fall armyworm pheromone (3-component lure; Scenturion, Clinton, WA) and contained insecticide strips (Hercon Environmental Co., Emigsville, PA). Traps were placed 22 January 2002, and collections were made at ≈2-wk intervals until 22 July 2003. This 18-mo test period allowed observations over two consecutive spring seasons when the northward migration is known to occur and should result in a decline in population numbers in the overwintering areas. Trapped moths were separated from other species and counted, and a subset (10–15) was randomly selected for polymerase chain reaction (PCR) analysis. Specimens were stored at −20°C after collection.

Trap-S was place on the west side of a large sod farm (235 ha) in northcentral Collier County (26°21.051′ N, 81°35.733′ W). Year-round sod production was composed of primarily St. Augustine grass [*Stenotaphrum secundatum* (Walt.) Kuntze], although there were sections of bahiagrass grown (*Paspalum notatum* Flugge.). These large turfgrass fields were bordered by areas of natural vegetation and a nursery containing trees and shrubs.

Trap-C was placed adjacent to a large sweet corn (*Zea mays* L.) field in southern Miami-Dade County (25°239.524′ N, 80°28.854′ W). Sweet corn production in Miami-Dade County averages close to 6,000 ha (Li et al. 2002a), with a planting season between early October and late January. Harvest is generally between January and May, and some growers produce two crops per season (October–December and January–May). Planting in this field occurred in October and December 2001–2003, with harvest in December and March 2002–2004. Many vegetable growers plant a cover crop of a sorghum × sudangrass hybrid (*Sorghum* bicolor L. Moench) from June to September, but the field adjacent to Trap-C was allowed to go fallow. For collections in November and December 2003, we wanted to extend the test area and obtain a high number of samples over the sampling period. In addition to Trap-C, which was kept in the original location, two other traps were used. Trap-C2 was placed within 150 m of Trap-C and adjacent to a sweet corn field. Trap-C3 (25°27.832′ N, 80°29.488′ W) was located ≈20 km east of Trap-C and adjacent to a sweet corn field.

Trap-T was located adjacent to a tomato field and across the road from a sweet corn field in southern Miami-Dade County (25°35.223′ N, 80°29.488′ W). Sweet corn was harvested soon after trap placement (February 2002), and the land was cleared for a residential subdivision. Tomato production in Miami-Dade County ranges between 1,500 and 5,500 ha, depending on season and markets, and fruit is harvested between December and May (Li et al. 2002b). Data for this trap was not obtained from 1 June 2002 to 1 July 2002 because of a defective trap and heavy rains. Trapping was discontinued after 8 July 2003 because of continued vandalism.

DNA Preparation. Individual adult moths were homogenized in 1 ml of homogenization buffer (0.03 M Tris-HCl at pH 8.0, 0.1 M NaCl, 0.2 M sucrose, 0.01 M EDTA at pH 8.0, and 0.5% Triton X-100) in a 5-ml Dounce homogenizer using either a hand pestle or a motorized mixer (Nagoshi and Meagher 2003). To remove large debris, the homogenate was filtered through a 5-ml plastic syringe plugged with cheese cloth (prewet with distilled water) into a 1.5-ml microfuge tube. The Dounce homogenizer was washed with 800 μl of buffer, which was filtered and added to the homogenate. Cells and nuclei were pelleted by centrifugation at 12,000 × *g* for 10 min at 4°C, and the supernatant was removed by aspiration. The pellet was resuspended in 600 μl nuclei buffer (0.01 M Tris-HCl at pH 8.0, 0.35 M NaCl, 0.1 M EDTA, and 1% *N*-lauryl sarcosine), and extracted with 400 μl phenol-

chloroform (1:1). The supernatant was transferred to a new 1.5-ml tube, precipitated with 400 μl isopropanol for 1 h at room temperature, and centrifuged at 12,000 × *g* for 10 min. The DNA pellet was washed with 70% ethanol and dried. The pellet was resuspended in 50 μl of distilled water, followed by purification using DNA Clean and Concentrator-5 columns (Zymo Research, Orange, CA) according to the manufacturer's instructions. Each PCR reaction used 1 μl of the DNA preparation (between 0.1 and 0.5 μg).

PCR Analysis. To determine strain identity from individual moths, genomic DNA from a randomly selected subset ($n \geq 10$) of the captured samples was tested by PCR for the mitochondrial *COI* gene restriction fragment-length polymorphism as described previously (Levy et al. 2002, Nagoshi and Meagher 2003). PCR amplification of genomic DNA was performed in a 50-μl reaction mix containing 5 μl 10× reaction buffer with $MgCl_2$ (Promega, Madison, WI), 1 μl 10 mM dNTP (New England Biolabs, Beverly, MA), 0.5 μl 20 μM primer mix, 1 μl DNA template, and 0.5 μl *Taq*DNA polymerase (Promega). Amplification of the *COI* gene used primers *JM76* (5′-GAGCTGAATTAGG(G/A)ACTCCAGG-3′) and *JM77* (5′-ATCACCTCC(A/T)CCTGCAGGATC-3′) and began with an initial incubation at 94°C (1 min), followed by 38 cycles of 94°C (1 min), 56°C (1 min), 72°C (1 min), and a final segment of 72°C for 5 min. On completion of PCR, 0.5 μl of *Msp*I was added to each reaction and incubated at 37°C for 1 h. Five microliters of gel loading buffer was added to each sample, and 20 μl was loaded on a 1.5% agarose gel. The R-strain (mt^R) pattern is a 569-bp PCR band, whereas the C-strain fragment (mt^C) is cut by *Msp*I to produce two fragments of 497 and 72 bp. Primers were synthesized by DNAgency (Malvern, PA).

Typically, ≈70–90% of the DNA preps gave useable PCR information. In collections where the strain identities of 10 or more samples were determined, the number of each strain present per night was extrapolated. This was obtained by first determining (by the PCR analysis of the representative subset) the percentage of each collection that was of one strain and multiplying that by the total number of males collected during the collection period. The product was divided by the number of nights in that period.

Results

Seasonal Capture Pattern. Trap captures from agricultural areas growing sweet corn (Trap-C) or a mixed crop of sweet corn and tomato (Trap-T) during the winter and spring seasons indicated that population peaks during the spring and fall, separated by an ~3- to 5-mo decline during the summer and a shorter depression in late winter (Fig. 1). In the period from February to the end of June 2002, an average of 58 moths per night was captured from the two traps. This was followed by a sharp decline from June to the end of July. Between 1 July and 15 October, trap captures had declined to an average of seven moths per night. Populations began to increase by the end of October 2002, regaining the spring highs in November and December (49 moths per night). There was a sharp but brief decline in January 2003 to an average of 18 moths per night, followed by a rapid increase in February 2003 continuing to June. The average during the period from February to June 2003 was 55 moths per night. This bimodal annual pattern with peaks in the spring and fall is consistent with previous studies examining pheromone traps placed in Dade and nearby Palm Beach counties (Pair et al. 1986).

Trap-S was located at a sod farm and was surrounded by extensive fields of turfgrass throughout the year. Despite the substantial differences in plant type, we observed a similar bimodal capture pattern as that recorded for Traps-C and -T, with March and April 2002 captures averaging 21 moths per night (Fig. 1). This was followed by a rapid decline during May and June and minimal captures from June to October (an average of two moths per night). A second peak was observed in November and December (15 moths per night average), followed by a mid-January decline (2 moths per night). Capture numbers increased again in the spring of 2003, with an average of 18 moths per night observed from February to April.

Host Strain Population Dynamics. We next determined the proportion of each host strain captured during the test period by PCR analysis of a strain-specific molecular marker (Fig. 2). The proportion of C-strain versus R-strain observed was used to estimate the numbers of each strain captured in the traps, displayed graphically as moths per night (Fig. 3). In the sod farm habitat surveyed by Trap-S, the R-strain predominated throughout the year (Fig. 3A). At no time did C-strain extrapolations exceed five moths per night, even during the spring and fall periods that had the highest fall armyworm density. From February 2002 to July 2003, only 11% (36/277) of the moths tested were of the C-strain, although at least one C-strain individual was observed in 14/28 collection periods tested.

A different strain distribution was observed with Traps-C and -T associated with vegetable crops. In the period from February to June 2002, 53% (130/243) of captured males tested were of the C-strain (Fig. 3B and C). A similar result of 44% (103/236) was obtained during the same period in 2003. This proportion did not change much during the summer depression from July to October, with 35% (48/139) of those tested showing the C-strain marker. This indicates that whatever was reducing capture numbers during this period was affecting both strains. In comparison, during the fall/winter growing season from October to January, the proportion of C-strain found in the traps declined to 13% (32/238). This reflected a substantial increase in the R-strain population, whereas C-strain captures remained low (Fig. 3A and B). Therefore, the spring capture peak represented an approximately equal mixture of both host strains, whereas the fall peak was limited to the R-strain.

The absence of an increase in the fall C-strain population was unexpected. To test whether the same pattern repeated itself in 2003, more extensive trap-

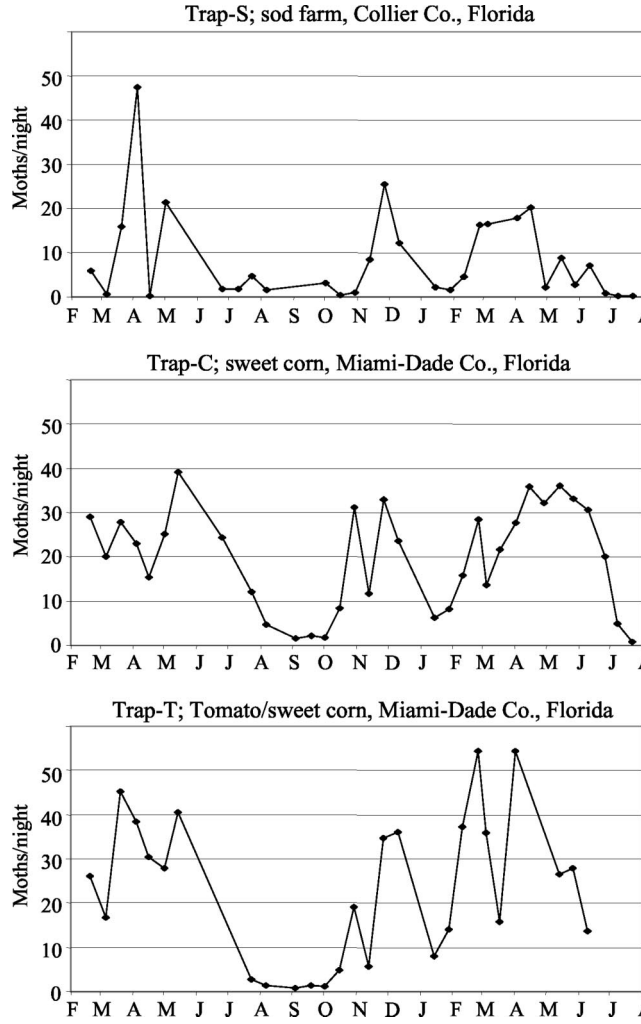

Fig. 1. Seasonal pheromone trap captures at selected locations in southern Florida, 2002–2003. Each data point represents total males captured divided by the number of evenings in the capture period. The initial sampling point is February 2002 and sampling concluded in July 2003.

ping was performed in agricultural areas during November and December 2003, a period in the previous year associated with high levels of fall armyworm infestation. In November and December 2003, the areas immediately adjacent to Trap-C contained vegetable crops (beans), with a large sweet corn field <100 m away. A second trap (C2) was located within 800 m of Trap-C, immediately adjacent to a sweet corn field with plants at various stages of development. A third trap (C3) was placed in another sweet corn field ≈20 km to the east, with most of the plants in the whorl stage. Consistent with the 2002 pattern, capture numbers in all traps were high during this period, indicating the presence of large and extensive fall armyworm populations (Table 1). In fact, Trap-C and -C2 showed the highest capture rates that we recorded over the past 2 yr. A minimum of 12 adult males from each collection was randomly selected and tested for strain identity, resulting in over 70 samples tested from each trap. In each sample period and for every trap, the C-strain was a minor component, never comprising >28% of the test group. Overall, a total of 319 males was analyzed, and 283 (89%) were of the R-strain. This was comparable with the results of contemporaneous captures at Trap-S (93% R-strain), a location where the C-strain was not expected to accumulate (Table 1). Therefore, as in 2002, the fall armyworm reinfestation of south Florida agricultural areas in fall/winter 2003 was not associated with substantial increases in the C-strain population, at least as determined by pheromone trapping.

Temperature and Rainfall. The pattern of adult captures was compared with weekly averages of maximum and minimum daily temperatures and precipitation (Fig. 3D and E). The general decline in trap captures beginning in June occurred coincident with the onset of minimum daily temperatures >20°C and the onset of the summer rainy season. Trap captures

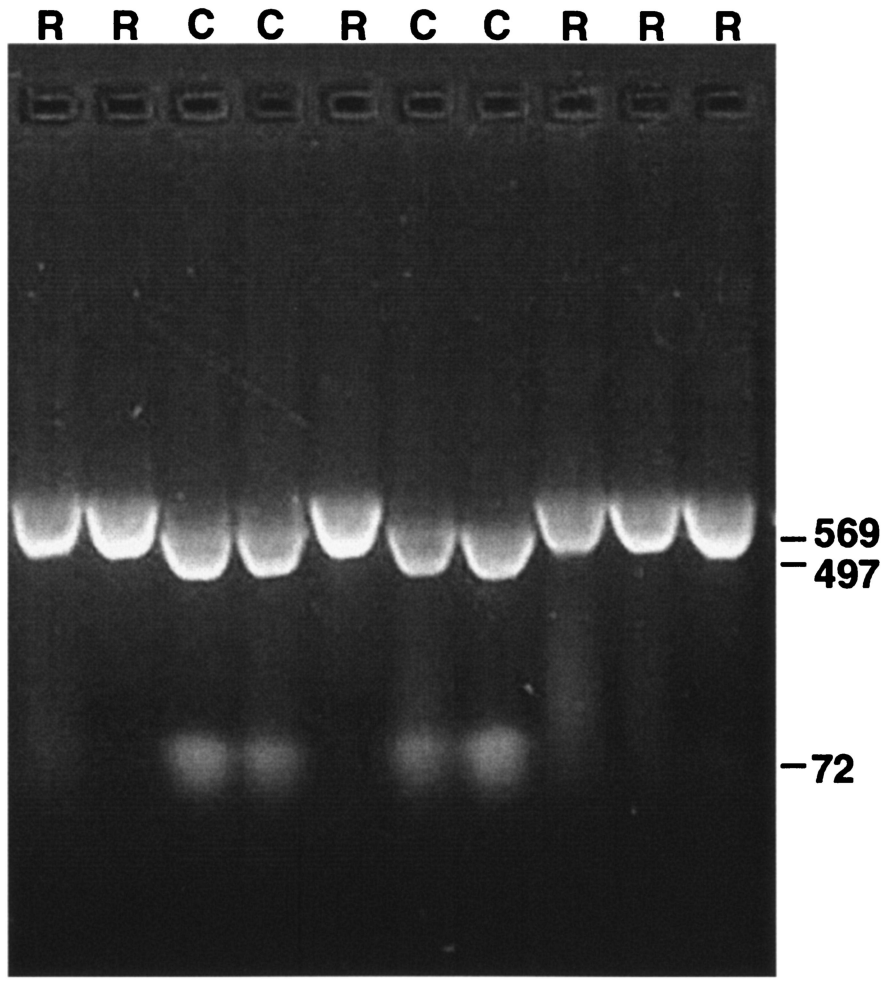

Fig. 2. Agarose gel displaying the diagnostic strain-specific DNA polymorphism used to distinguish between rice- and corn-strains. DNA from 10 moths collected from Trap-C was individually amplified by PCR using a primer combination specific for a portion of the mitochondrial *COI* gene that contains a strain-specific *Msp*I site. After digestion with *Msp*I, a single band (569 bp) indicates the absence of the *Msp*I site, a characteristic of the rice-strain (R). Two smaller bands (497 and 72 bp) are produced if the *Msp*I site is present, indicating a corn-strain (C) identity. The gel is stained with ethidium bromide and photographed under UV illumination.

of the R-strain did not recover until October, corresponding with the decline in average minimum daily temperature to below 20°C. The mid-January decline in numbers coincided with a sharp drop in minimum daily temperatures to 5°C and below. This was followed by an increase in the number of both strains as the average daily temperature rose in February, although the recovery of the C-strain may have occurred 1–2 wk after that of the R-strain (Fig. 3A and B).

We anticipated that the density of the C-strain population would largely reflect the agricultural activities in the neighboring fields. Sweet corn was planted in southern Miami-Dade County (Homestead) near Trap-C from October to mid-December in 2001 and 2002. Crops were harvested beginning late December, and harvesting was completed by May in both 2002 and 2003. Despite the presence of whorl-stage sweet corn through most of the fall, the number of trapped C-strain males did not increase until February, shortly after the lowest temperatures of the season, with peaks in March and April (Fig. 3A). Relatively high numbers of C-strain males continued to be captured until June, suggesting that the postharvest cover crop of sorghum/sudangrass might be able to provide a satisfactory habitat to support one to two additional generations. Both strains showed minimal capture levels by the end of July. Most tomatoes near Trap-T were planted from September to early January, with harvest being generally completed by May. This was followed by a sharp decline in trap captures. As with Trap-C, capture numbers for both strains were at minimal levels by July. These results indicate that trap captures for both strains declined from their spring peak within

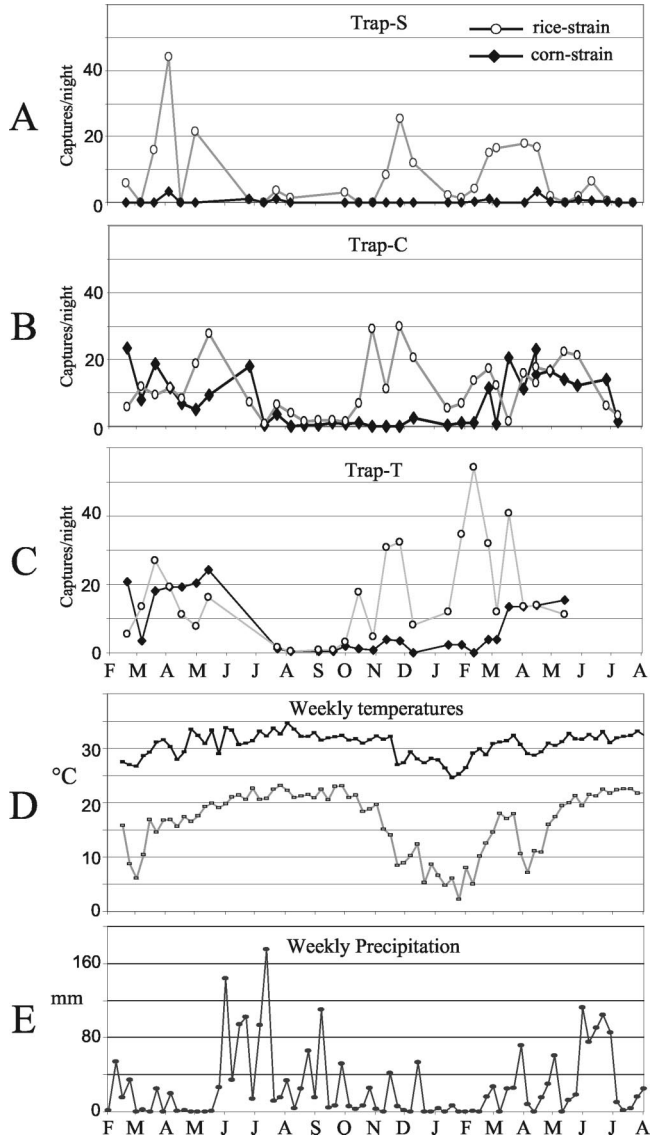

Fig. 3. Distribution of host strains collected from pheromone traps compared with average weekly temperatures and weekly rainfall. (A–C) The strain composition of each collection was determined by PCR and used to calculate the average number of each strain present per night during each collection period. Gray lines with open circles denote R-strain collections. Black lines with black diamonds denote C-strain numbers. (D) Average air temperatures recorded for the Homestead, FL area during the testing period. Upper curve reflects the maximum daily temperature; lower curve reflects the minimum daily temperature. The squares denote weekly averages. (E) Weekly rainfall (in millimeters) recorded for the Homestead, FL region during the testing period. The weather data were obtained from the University of Florida Institute of Food and Agricultural Sciences. The initial sampling point is February 2002, and sampling was concluded in July 2003.

a month of each other, providing no clear evidence for strain differences in the timing of the northward migration after the spring harvest.

Discussion

Pheromone traps are a convenient means of obtaining a "snapshot" of the adult fall armyworm population density at a given time and place (Pair et al. 1986, Mitchell et al. 1991). Captured male adults will reflect both the local resident population as well as transients migrating through the region. As such, they can provide a dynamic picture of short-term changes in adult population in a proscribed area. In addition, trap captures directly measure the number of mating-receptive males within range of a pheromone source, thereby indicating periods of high mating potential that could portend subsequent increases in larval infestation. However, there is indirect evidence that

Table 1. Fall armyworm males collected during November and December 2003 in pheromone traps placed in agricultural areas

Trap	Collection period	Moths/night/trap	No. tested	No. rice-strain	Percent rice-strain
C	11/19–11/20	165.0	16	15	94
	11/21–11/25	142.7	27	27	100
	11/26–12/2	75.7	15	14	93
	12/3–12/9	36.6	16	15	94
	12/10–12/14	111.0	18	17	94
C2	11/19–11/20	93.0	34	32	94
	11/21–11/25	154.4	16	15	94
	11/26–12/2	121.3	37	32	86
	12/3–12/9	81.9	18	13	72
	12/10–12/14	138.2	16	14	88
C3	11/19–11/20	7.0	14	11	79
	11/21–11/25	25.3	33	30	91
	11/26–12/2	17.1	16	13	81
	12/3–12/9	13.6	14	11	79
	12/10–12/14	12.3	29	24	83
C1–3	11/19–12/14	80 (average)	319	283	89%
S	11/21–11/24	16.6	17	15	88
	11/25–12/1	9.6	14	13	93
	12/2–12/8	17.7	32	32	100
	12/9–12/15	13.8	12	10	83
Total	11/21–12/15	14 (average)	75	70	93%

commercial pheromones may not be equally attractive to the two strains, potentially biasing estimates of strain proportions (Pashley et al. 1992). We note that such a bias, if it exists, should not affect the significance of our observed geographical or seasonal differences in strain capture ratios, because all comparisons were made from samples obtained using the same trapping system.

The bimodal seasonal distribution of moth captures in southern Florida has been previously described (Pair et al. 1986, Mitchell et al. 1991). Our data indicate that for at least 2002 and 2003, this bimodal pattern was the result of two subpopulations undergoing very different seasonal behaviors. Specifically, C-strain males were captured in significant numbers only during the spring season, with the fall peak due almost entirely to the R-strain. While a multiyear and geographically broader survey is required to establish the generality of these strain-specific patterns, our results indicate that the host strains can differ significantly in their temporal distribution in Florida overwintering habitats, suggesting significant strain-specific differences in response to seasonal conditions.

The observation that the sod farm area (Trap-S) displayed the same bimodal population distribution as the agricultural traps (Trap-C and -T) suggests that this seasonal pattern was not caused by competition with the C-strain or to the cycle of sweet corn planting and harvesting, but rather is a response to some environmental factor common to the different habitats. The July-to-October decline in R-strain capture numbers was observed in all three locales tested, even though they differed substantially in plant composition. This bimodal seasonality had been previously observed and was attributed to the effects of the pronounced wet-dry seasons characteristic of subtropical and tropical areas on plant quantity and quality (Pair et al. 1986). For example, in studies performed in Mexico, high capture rates tended to occur 60–90 d after rainfall peaks, whereas intervals of least capture most frequently occurred 60–90 d after periods of least rainfall (Raulston et al. 1986). Such a mechanism could explain our observation of a peak in R-strain capture in the fall and winter months that followed the summer rainy season, but is not consistent with the spring peak in captures that followed the winter dry season (Fig. 3). Even more problematic is the behavior of the C-strain for which there was no evidence of a population increase in the fall resulting from the summer rainy season.

Another possibility is that the decline in capture numbers during the year may be related to extremes in the daily minimum temperature. Fall armyworm captures for both strains are lowest when the daily minimum temperature rises above 20°C (July–October) or below 5°C (January). There is precedence for correlations between daily temperature and field capture numbers for other insects (Butler et al. 1999, Cammell and Knight 1992, Scott et al. 2000, Souza and Carvalho 2002). Of particular interest are field studies indicating that the population of *Chrysoperla externa* (Hagen) in citrus orchards is negatively affected by increases in the minimum daily temperature (Souza and Carvalho 2002). The significance of this coincidence with fall armyworm is unknown but could be explained if an important behavior, such as mating or flight activity, is deleteriously affected by seasonal temperature extremes.

When temperatures and rainfall moderated in the fall, the incidence of R-strain captures increased dramatically, comprising the majority of the moths trapped during this period. Why the C-strain did not behave similarly is unknown. The most obvious expected influence on the C-strain population is the pattern of sweet corn planting and harvesting. However, although sweet corn was grown in the agricultural trap areas from October to May, C-strain numbers did not increase until February. Apparently, the

presence of its preferred host plant and environmental conditions conducive to expansion of the R-strain population were not sufficient to stimulate C-strain increases during the fall.

The increase in moth capture numbers during the fall months is typical for southern Florida and Texas and was shown to correlate with weather and wind conditions conducive to southward migration (Pair et al. 1986, Pair et al. 1987, Mitchell et al. 1991). This led to the suggestion of a north-to-south return migration to overwintering sites before the winter freeze. However, our observations suggest that only the R-strain population increases in the fall, implying strain-specific migration behavior. If this is the case, it leaves open the question of what is the source of the C-strain population that suddenly appears in the spring. Some possible explanations include the following: (1) the depleted local population is poised for a rapid expansion when favorable conditions (specific to the spring season) arise, (2) trap captures during the fall (for unknown reasons) significantly underestimate the local C-strain population, or (3) there is an unidentified habitat in southern Florida that can serve as a winter reservoir for the C-strain. Studies to test these possibilities are currently underway.

In summary, we showed that combining pheromone-trapping techniques with molecular methods for determining host strain identity can provide unexpected and important advances to our understanding of fall armyworm population behavior. Evidence is provided that indicates that, while the two strains can be sympatric, they also can differ substantially in their response to seasonal changes, varying in both population numbers and geographic distribution. We are in the process of additional long-term field studies to define other strain-specific differences in population behavior in the wild and to identify habitats that could serve as reservoirs for maintaining populations, particularly the C-strain, during the less optimal seasons. Such information is essential for the development of areawide strategies to mitigate the overwintering and migrating capacities of one or both strains.

Acknowledgments

We thank J. Sharp for excellent technical support. We thank J. Shapiro (USDA) and G. Nuessly (University of Florida) for helpful comments on the manuscript. Voucher specimens (FSCA–EE'04, V01–10) were placed in the Museum of Entomology, Florida State Collection of Arthropods, Florida Department of Agriculture and Consumer Services, Division of Plant Industry, Gainesville, FL. The use of trade, firm, or corporation names in this publication is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the United States Department of Agriculture or the Agricultural Research Service of any product or service to the exclusion of others that may be suitable.

References Cited

Adamczyk, J. J., Jr., J. W. Holloway, B. R. Leonard, and J. B. Graves. 1997. Susceptibility of fall armyworm collected from different plant hosts to selected insecticides and transgenic Bt cotton. J. Cotton Sci. 1: 21–28.

Butler, L., V. Kondo, E. M. Barrows, and E. C. Townsend. 1999. Effects of weather conditions and trap types on sampling for richness and abundance of forest macrolepidoptera. Environ. Entomol. 28: 795–811.

Cammell, M. E., and J. D. Knight. 1992. Effects of climatic change on the population dynamics of crop pests. Adv. Ecol. Res. 22: 117–162.

Greene, G. L., M. J. Janes, and F. W. Mead. 1971. Fall armyworm, *Spodoptera frugiperda,* males captured at three Florida locations in traps baited with virgin females. Fla. Entomol. 54: 165–166.

Jamjanya, T., S. S. Quisenberry, S. S. Croughan, and R. N. Story. 1990. Comparison of bermudagrass lines grown in different cultural conditions and the effect on screening for fall armyworm (Lepidoptera: Noctuidae) resistance. J. Econ. Entomol. 83: 585–590.

Knipling, E. F. 1980. Regional management of the fall armyworm-a realistic approach? Fla. Entomol. 63: 468–480.

Levy, H. C., A. Garcia-Maruniak, and J. E. Maruniak. 2002. Strain identification of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) insects and cell line: PCR-RFLP of cytochrome oxidase subunit I gene. Fla. Entomol. 85: 186–190.

Li, Y. C., H. H. Bryan, W. Klassen, M. Lamberts, and T. Olczyk. 2002a. Sweet corn production in Miami-Dade County, Florida. Univ. of Florida, Florida Coop Ext. Serv., IFAS, HS-862, 2 pp.

Li, Y. C., H. H. Bryan, W. Klassen, M. Lamberts, and T. Olczyk. 2002b. Tomato production in Miami-Dade County, Florida. Univ. of Florida, Florida Coop Ext. Serv., IFAS, HS-858, 3 pp.

Lu, Y. J., and M. J. Adang. 1996. Distinguishing fall armyworm (Lepidoptera: Noctuidae) strains using a diagnostic mitochondrial DNA marker. Fla. Entomol. 79: 48–55.

Lu, Y., M. J. Adang, D. J. Eisenhour, and G. D. Kochert. 1992. Restriction fragment length polymorphism analysis of genetic variation in North American populations of the fall armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae). Mol. Ecol. 1: 199–208.

Lu, Y. J., G. D. Kochert, D. J. Isenhour, and M. J. Adang. 1994. Molecular characterization of a strain-specific repeated DNA sequence in the fall armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae). Insect Mol. Biol. 3: 123–30.

Luginbill, P. 1928. The fall armyworm. U.S. Dep. Agric. Tech. Bull. 34: 1–91.

McMichael, M., and D. P. Prowell. 1999. Differences in amplified fragment-length polymorphisms in fall armyworm (Lepidoptera: Noctuidae) host strains. Ann. Entomol. Soc. Am. 92: 175–181.

Meagher, R. L., and M. Gallo-Meagher. 2003. Identifying host strains of fall armyworm (Lepidoptera: Noctuidae) in Florida using mitochondrial markers. Fla. Entomol. 86: 450–455.

Mitchell, E. R. 1979. Migration by *Spodoptera exigua* and *S. frugiperda,* North American style, pp. 386–393. *In* Movement of highly mobile insects: concepts and methodology in research, R. L. Rabb, and G. G. Kennedy, (eds.). University Graphics, North Carolina State University, Raleigh, NC.

Mitchell, E. R., J. N. McNeil, J. K. Westbrook, J. F. Silvain, B. Lalanne-Cassou, R. B. Chalfant, S. D. Pair, V. H. Waddill, A. Sotomayor-Rios, and F. I. Proshold. 1991. Seasonal periodicity of fall armyworm, (Lepidoptera: Noctuidae) in the Caribbean Basin and northward to Canada. J. Entomol. Sci. 26: 39–50.

Nagoshi, R. N., and R. Meagher. 2003. FR tandem-repeat sequence in fall armyworm (Lepidoptera: Noctuidae) host strains. Ann. Entomol. Soc. Am. 96: 329–335.

Pair, S. D., J. R. Raulston, A. N. Sparks, J. K. Westbrook, and G. K. Douce. 1986. Fall armyworm distribution and population dynamics in the southeastern states. Fla. Entomol. 69: 468–487.

Pair, S. D., J. R. Raulston, D. R. Rummel, J. K. Westbrook, W. W. Wolf, A. N. Sparks, and M. F. Schuster. 1987. Development and production of corn earworm and fall armyworm in the Texas high plains: evidence for reverse fall migration. Southwest Entomol. 12: 89–99.

Pashley, D. P. 1986. Host-associated genetic differentiation in fall armyworm (Lepidoptera: Noctuidae): a sibling species complex? Ann. Entomol. Soc. Am. 79: 898–904.

Pashley, D. P. 1988. The current status of fall armyworm host strains. Fla. Entomol. 71: 227–234.

Pashley, D. P. 1989. Host-associated differentiation in armyworms (Lepidoptera: Noctuidae): an allozymic and mitochondrial DNA perspective, pp. 103–114. *In* H. D. Loxdale and J. der Hollander (eds.), Electrophoretic studies on agricultural pests. Clarendon Press, Oxford, UK.

Pashley, D. P., and J. A. Martin. 1987a. Reproductive incompatibility between host strains of the fall armyworm (Lepidoptera: Noctuidae). Ann. Entomol. Soc. Am. 80: 731–733.

Pashley, D. P., S. J. Johnson, and A. N. Sparks. 1985. Genetic population structure of migratory moths: the fall armyworm (Lepidoptera: Noctuidae). Ann. Entomol. Soc. Am. 78: 756–762.

Pashley, D. P., A. M. Hammond, and T. N. Hardy. 1992. Reproductive isolating mechanisms in fall armyworm host strains (Lepidoptera: Noctuidae). Ann. Entomol. Soc. Am. 85: 400–405.

Pashley, D. P., S. S. Quisenberry, and T. Jamjanya. 1987b. Impact of fall armyworm (Lepidoptera: Noctuidae) host strains on the evaluation of bermudagrass resistance. J. Econ. Entomol. 80: 1127–1130.

Pashley, D. P., T. C. Sparks, S. S. Quisenberry, T. Jamjanya, and P. F. Dowd. 1987. Two fall armyworm strains feed on corn, rice, and bermudagrass. Louisiana Ag. 30: 8–9.

Quisenberry, S. S., and F. Whitford. 1988. Evaluation of bermudagrass resistance to fall armyworm (Lepidoptera: Noctuidae): influence of host strain and dietary conditioning. J. Econ. Entomol. 81: 1463–1468.

Raulston, J. R., S. D. Pair, A. N. Sparks, J. G. Loera, F.A.M. Pedraza, A. T. Palamon, A. Ortega, J. M. Sanchez Ruiz, P. C. Marquez, H. A. Rueles, J. M. Perez, R. R. Rodriguez, H. R. Carrillo, R. R. Archundia, and R. F. Herrera. 1986. Fall armyworm distribution and population dynamics in the Texas-Mexico Gulf Coast area. Fla. Entomol. 68: 686–691.

Scott, T. W., A. C. Morrison, L. H. Lorenz, G. G. Clark, D. Strickman, P. Kittayapong, H. Zhou, and J. D. Edman. 2000. Longitudinal studies of *Aedes aegypti* (Diptera: Culicidae) in Thailand and Puerto Rico: population dynamics. J. Med. Entomol. 37: 77–88.

Snow, J. W., and W. W. Copeland. 1969. Fall armyworm: use of virgin female traps to detect males and to determine seasonal distribution. USDA Prod. Res. Rep. 110, p. 9.

Souza, B., and C. F. Carvalho. 2002. Population dynamics and seasonal occurrence of adults of *Chrysoperla externa* (Hagen, 1861) (Neuroptera: Chrysopidae) in a citrus orchard in Southern Brazil. Acta Zool. Acad. Sci. Hungaricae. 48: 301–310.

Sparks, A. N. 1979. A review of the biology of the fall armyworm. Fla. Entomol. 62: 82–86.

Veenstra, K. H., D. P. Pashley, and J. A. Ottea. 1995. Host-plant adaptation in fall armyworm host strains: comparison of food consumption, utilization, and detoxication enzyme activities. Ann. Entomol. Soc. Am. 88: 80–91.

Whitford, F., S. S. Quisenberry, T. J. Riley, and J. W. Lee. 1988. Oviposition preference, mating compatibility, and development of two fall armyworm strains. Florida Entomol. 71: 234–243.

Received 14 January 2004; accepted 6 May 2004.